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Geographic Distribution of the San Juan Ichthyofauna of Central America with Remarks on its Origin and Ecology

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INTRODUCTION

The scientific study of fishes of the Great Lakes of Nicaragua began in 1864 with the description by Günther of *Heros labiatus* (=*Cichlasoma labiatum*) from Lake Managua. Subsequently, Günther reported on several other species collected in the Great Lakes by Captain J. M. Dow. Astorqui (1967) reviewed the sparse ichthyological literature dealing with Nicaraguan fishes and pointed out the paucity of recent studies. Since then Villa (1971) has produced a provisional list of the freshwater and brackish water fishes of Nicaragua and Astorqui (1972) has analyzed the ichthyofauna of the Great Lakes Basin. Riedel (1972) discussed the geological history of the Great Lakes in relation to the composition and evolution of its fish fauna.

The present paper analyzes the existing distribution and ecology of the lower Central American ichthyofauna, in light of paleogeologic knowledge, in order to determine the derivation of historical faunal elements, the barriers responsible for subdivision of these ancestral ichthyofaunas, and the subsequent dispersal which has resulted in secondary distributions of the descendent species in the San Juan Fish Province. For the purposes of this analysis, only freshwater fishes (*i.e.*, species of non-marine affinity) are utilized.

FISH PROVINCES OF CENTRAL AMERICA

The present state of distributional and systematic knowledge of the Middle American ichthyofauna now permits major fish provinces to be outlined, although a revision of one major taxon (*Rhamdia*) may modify the number of species components somewhat.

In preparing an analysis of faunal provinces, I have relied heavily on Miller's (1966) data for fish distribution in northern Middle America and for his tentative delimitation of the northern boundaries of the Usumacinta and Chiapas-Nicaraguan Provinces. The Panamanian drainage systems delineated by Loftin (1965) and his distributional data, modified by subsequent study of some of the material, were incorporated in the analysis. A geographic analysis of Honduran fishes by Martin (1972), based on extensive collections from both Atlantic and Pacific versants, was crucial in the study. Other critical collections from previously uncollected localities in Nicaragua were generously donated by Jaime Villa and supplemented by my own collections from central and southern Nicaragua. Collections made in Central America since 1961 to the present, by numerous collectors, provided knowledge of Costa Rican fish distribution (Bussing, 1967) and establish limited additions to the ichthyofauna of other Central American republics.

Recent collections on the Atlantic versant of Honduras and Nicaragua reveal a depauperate ichthyofauna with little endemism. The San Juan Assemblage clearly extends to northern Nicaragua before merging with a marginal Usumacinta fauna. Collections from Panamá and Costa Rica also reveal that the southern limit of the San Juan Province lies southward in Panamá.

Provisional province limits were placed where considerable faunal changes occur in the assemblages of adjacent watersheds. Species were then assigned to one or more provinces on the basis of their distribution, and the totals compiled by drainage basin. Interpolation was applied in these charts where known distributions were discontinuous. Final placement of province limits was then made and all species were reassigned to provinces on the basis of this last judgment.

In addition to the above empirical method, a computer analysis was applied to the same distributional data of the principal Atlantic drainages between eastern Guatemala and eastern Panamá (Table 1 and Fig. 1). Drs. Jay M. Savage and Ian R. Straughan of the Allan Hancock Foundation, University of Southern California, applied a Polythetic Aglomerative Classification using the similarities indexes of Czekanowski or Jaccard and the flexible sorting strategy, normal (site site) analysis and inverse (species species) analysis. Results were determined from a dendrogram that shows the degree of similarity between these groups of drainage basins. The results confirm the significance of the faunal boundaries recognized by the intuitive approach, but reveal that the Usumacinta-San Juan boundary was incorrectly placed. The faunal boundaries are as follows in descending order of significance: 1) a major discontinuity between the San Juan and Isthmian Provinces, 2) a very significant discontinuity between the San Juan and Usumacinta Provinces, 3) a significant discontinuity between the Río Motagua and Ulua basins, 4) significant discontinuities between the Río Coclé Norte and Chagres basins and Chagres and San Blas watersheds of the Isthmian Province. On the basis of these results, Table 1 was prepared to show for each drainage the total number of species and the number of these which also occur in the other drainages (*i.e.*, the degree of affinity between the species of each basin and each of the provinces). For example, there are 46 freshwater species known from the San Juan basin; all by definition are members of the San Juan Province; 20 of these also occur in the Usumacinta Province and 7 in the Isthmian Province (Table 1).

Usumacinta Province.—Miller (1966) delimited the province and discussed its ichthyofauna. In the present arrangement, the province is extended to include the entire

TABLE 1. Distribution of freshwater fishes by Atlantic drainages from southern Guatemala to eastern Panamá. The total number of species per drainage is given first, followed by the number of species of each drainage represented in each of the other Central American Fish Provinces. The abbreviations to the left of each drainage refer to the map symbols in Figure 1.

		Drainage	Total species	Usumacinta	San Juan	Isthmian
Usumacinta	PO	Polochic	30	30	11	5
	MO	Motagua	31	31	14	5
	UL	Ulua	26	26	17	6
	LA	La Ceiba	23	23	15	6
	AG	Aguan	23	23	18	6
	PL	Paulaya	19	19	16	6
	PT	Patuca	21	21	18	6
	CO	Coco	23	23	20	6
San Juan	PR	Prinzapolka	24	20	24	6
	ES	Escondido	24	19	24	6
	SJ	San Juan	46	20	46	7
	CR	Chirripó	30	17	30	7
	PA	Parismina	27	16	27	7
	MA	Matina	24	15	24	7
	SI	Sixaola	18	12	18	9
	CH	Changuinola	18	11	18	10
	LC	L. Chiriquí	19	10	19	11
	GM	G. Mosquitos	18*	?	?	?
Isthmian	CN	Coclé Norte	17	6	11	17
	CG	Chagres	33	6	11	33
	SB	San Blas	25	4	9	25

*By interpolation

Atlantic versant of Honduras and northern Nicaragua to between the Río Coco and Prinzapolka drainages (Fig. 1). On the basis of this delimitation, 130 species representing 34 genera and 10 families of freshwater fishes occur in the province.

Clearly a subprovince is indicated between the Río Motagua and Río Coco drainages, but this depauperate region harbors no distinctive major fauna nor the endemic forms which would permit a major province rank.

Isthmian Province.—On the basis of the computer analysis, the northern Atlantic boundary of this province lies between Peninsula Valiente (forming part of Laguna de Chiriquí) and Río Coclé del Norte, Panamá. Loftin (1965) noted the shift in faunas between adjacent watersheds, and pointed out the critical importance of this entirely unknown region. The area is about 130 km long and comprises numerous independent coastal streams emptying into the Golfo de los Mosquitos. Collections will probably reveal that the region is a broad filter-barrier.

Unlike the Atlantic slope boundary of the Isthmian Province, which represents a biological filter-barrier created by a merging of discrete faunas over a rather monotonous physical environment, the Isthmian assemblage reaches an exceptionally sharp terminus on the Pacific slope at Punta Mala (Punta Judas), Costa Rica. Just north of this point several coastal ranges extend to the sea creating an impressive physical barrier that eliminates the coastal swamp environment as a dispersal route for freshwater species. This terminus also marks a climatic and corresponding vegetation barrier for the herpetofauna (Stuart, 1966; Savage, 1966). The Pirrís drainage system of Costa Rica, which contains numerous coastal streams and a few rivers of moderate size, extends from the Río Grande de Térraba in the south to Punta Mala near the mouth of the Golfo de Nicoya (López, 1972). Many Isthmian freshwater species drop out in this region and widespread Central American species aside, only one Isthmian species reaches the Tárcoles drainage to the north. No Chiapas-Nicaraguan species reach the Pirrís drainage except ubiquitous forms which extend along the entire Pacific slope. A more detailed treatment of Costa Rican zoogeography will be presented elsewhere.

Between the northern limits mentioned and the southern border of Panamá, 97 species representing 51 genera and 12 families of freshwater fishes occur in the Isthmian Province.

Chiapas-Nicaraguan Province.—North of the Punta Mala promontory, the narrow Pacific coastal plain receives much less rainfall than southern Costa Rica or the Atlantic lowlands. I have not analyzed this faunal assemblage in detail, but some observations are pertinent to an understanding of the San Juan ichthyofauna. This area, as delimited by Miller (1966) and modified by the present study, certainly qualifies as a fish province. Depauperate as it is, endemism is marked and several species are autochthonous. Forty-five species representing 18 genera and 9 families of freshwater fishes occur in the region. It must be pointed out however, that at least 14 of the 45 known species are primarily Atlantic forms that have gained access to the Pacific slope through several dispersal routes in the southern part of the province. Few of these species are widely distributed on the Pacific versant, which suggests recent arrival, competition with better adapted species, and/or difficulty in surviving in a region subject to xeric climate.

From south to north, the following areas are affected by Atlantic faunal intrusion:

1) The Río Bebedero and Río Tempisque drainages of Guanacaste Province, Costa Rica contain two widespread species of Atlantic origin, *Cichlasoma dovii* and *C. longimanus*, and four species of restricted distribution, *Cichlasoma alfari, Herotilapia multispinosa, Alfaro cultratus* and *Rivulus isthmensis*. The headwaters of the Río Tempisque pass within 200 meters of Atlantic tributaries of the Río Sapoá at 400 meters elevation on the slopes of Volcán Orosí. The Río Blanco, a tributary of the Río Bebedero is separated by a swamp at 560 meters elevation from the Río Negro, a tributary of Lake Nicaragua. It is presumed that either or both of these areas serve, or have served in the recent past, as dispersal routes for freshwater organisms.

2) Affluents of the Río Tamarindo on the Pacific slope of Nicaragua are separated from Lake Managua by a narrow strip of land rising about 20 to 30 meters above lake level. This drainage contains five Atlantic species, *Cichlasoma dovii, C. longimanus, C. friedrichsthalii, C. managuense* and *Neetroplus nematopus*. The last three species do not seem to have spread to immediately adjoining watersheds.

3) The Estero Real drains the northern end of the Nicaragua Depression and empties into the lower end of the Golfo de Fonseca. This watershed contains three Atlantic species, *Cichlasoma centrarchus, Herotilapia multispinosa* and *Lepisosteus tropicus* (Fig. 2). Either the Tamarindo or Estero Real drainage has probably been connected with Lake Managua in the past. The possibility of human agents in effecting this transfer of fishes cannot be discounted, however.

4) Three Atlantic species, *Brycon guatemalensis* (Fig. 3), *Cichlasoma longimanus* and *Lepisosteus tropicus* (Fig. 2) appear in the Pacific drainages of Honduras, and Martin (1972) suggested as dispersal routes possible connections between

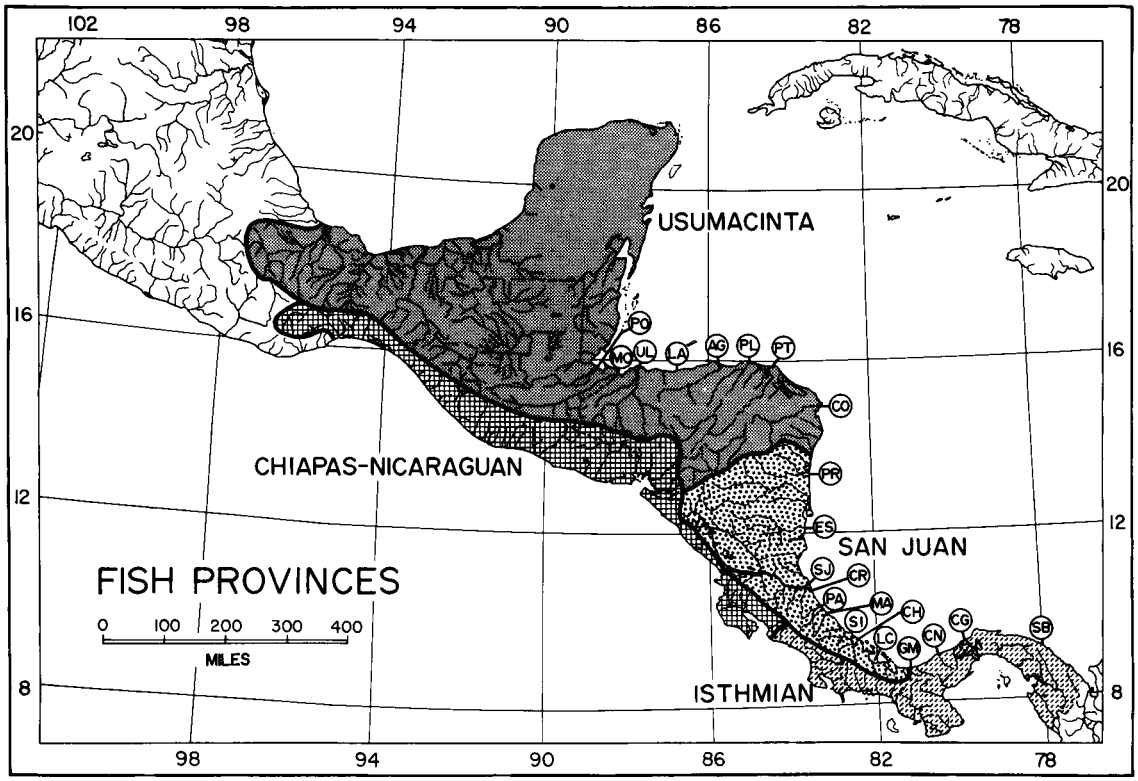

FIG. 1. Distribution of the Middle American ichthyofauna by major fish provinces. See Table 1 for key to drainage symbols.

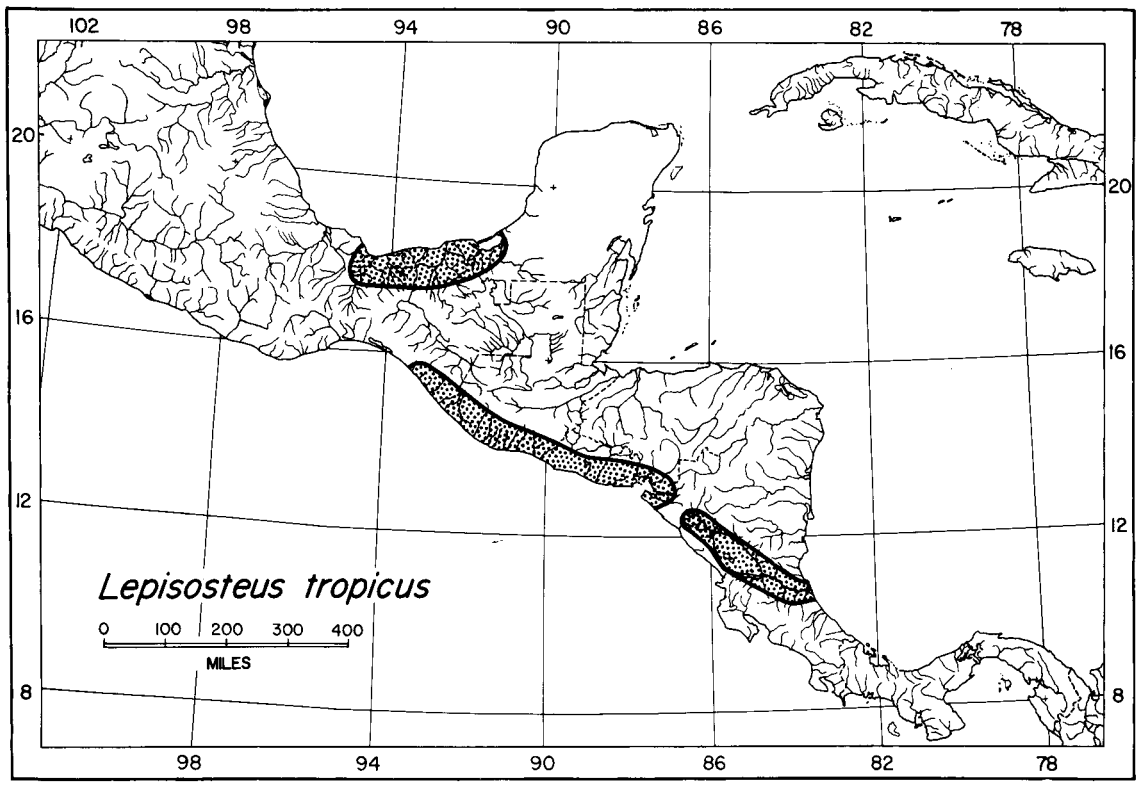

FIG. 2. Range of *Lepisosteus tropicus*. An example of a Northern Element. The species probably reached the Pacific versant by stream capture across the Isthmus of Tehuantepec and reinvaded the Atlantic slope where it is restricted to the San Juan watershed. Modified after Miller (1966) and Gilbert and Kelso (1971).

the Río Ulua and Goascorán and the Río Patuca and Choluteca. Both the Río Goascorán and Choluteca flow into the Golfo de Fonseca, as does the Estero Real. *Poeciliopsis gracilis*, probably of Pacific origin, is known from near Oaxaca, México to Río Tamarindo, Nicaragua (Fig. 4) It probably reached the Atlantic versant through one of the Golfo de Fonseca routes.

The San Juan Ichthyofauna

Regan (1906–08), on the basis of collections then available, created the San Juan Province to include only the San Juan watershed which is shared by Nicaragua and Costa Rica. Miller (1966) did not attempt to alter Regan's province in view of the poorly known Honduran and Nicaraguan ichthyofaunas. The new limits of the San Juan Province proposed in this paper, have been mentioned above in conjunction with adjoining provinces and include the Atlantic slope watershed from the Río Prinzapolka, Nicaragua to the Golfo de los Mosquitos in western Panamá.

As here conceived, 54 species representing 25 genera and families of freshwater fishes occur in the San Juan Province. Species of marine affinity (most of which are presumably euryhaline), recorded from freshwaters in the province, number at least 84. The greatest diversity is found in the San Juan drainage itself where 46 freshwater species occur (Table 1). Thirty-two of these species are found in the Great Lakes proper (Table 2). Fourteen other San Juan forms have been collected in affluents to the lakes or tributaries of the Río San Juan. Some of these non-lake species, especially those found in lake affluents, probably occur from time to time in the lakes. Among the lake-excluded species (Table 2), the poeciliids, *Brachyrhaphis parismina* and *Priapichthys annectens*, and a cichlid, *Cichlasoma tuba*, are fluviatile species and would not be expected in the Great Lakes proper. Apparently they have not even been able to transgress the lakes and reach their affluents.

The catfishes, *Rhamdia nicaraguensis* (possibly a synonym of *Rhamdia guatemalensis*) and *R. underwoodi* are well adapted to moving or standing waters but are presumably displaced by the specialized lake forms, *Rhamdia barbata, R. managuensis* and *Rhamdia* sp. The poeciliids, *Brachyrhaphis holdridgei* and *Phallichthys amates* occur most abundantly in small slow-moving waters or swamps. The latter poeciliid should turn up in future lake collections when the "estero" environment of Lake Nicaragua is more intensively studied. *B. holdridgei* preys largely on insects which fall into its habitat from surrounding vegetation and would not be expected in the lake environment. *Poecilia* cf *sphenops* and *Poeciliopsis gracilis* are found in affluents of the lakes and are common littoral inhabitants of other lakes. They may be found in future lake collections.

The cichlids, *Cichlasoma septemfasciatum*[1] and *C. alfari*, are common in tributaries of the Río San Juan, but their frequency in the San Juan proper is not known. As in the case

Table 2. List of freshwater fishes of the Río San Juan drainage basin, including fishes of marine affinity known from Lakes Nicaragua or Managua. Species not reported from the lakes proper are marked with an asterisk.

Freshwater Species

Characidae "Sardinas"
- *Astyanax fasciatus* (Cuvier)
- *Astyanax nasutus* Meek
- *Bramocharax bransfordii* Gill
- *Brycon guatemalensis* Regan
- **Bryconamericus scleroparius* (Regan)
- *Hyphessobrycon tortuguerae* Böhlke
- *Carlana eigenmanni* (Meek)
- *Roeboides guatemalensis* (Günther)

Gymnotidae
- **Gymnotus cylindricus* LaMonte

Pimelodidae "Chulines, Barbudos"
- *Rhamdia barbata* Meek
- *Rhamdia managuensis* (Günther)
- *Rhamdia nicaraguensis* (Günther)
- **Rhamdia underwoodi* Regan
- *Rhamdia* sp.

Lepisosteidae "Gaspares"
- *Lepisosteus tropicus* (Gill)

Cyprinodontidae
- **Rivulus isthmensis* Garman

Poeciliidae "Olominas, Pepescas"
- *Alfaro cultratus* (Regan)
- *Belonesox belizanus* Kner
- **Brachyrhaphis holdridgei* Bussing
- **Brachyrhaphis parismina* (Meek)
- *Gambusia nicaraguensis* (Günther)
- *Neoheterandria umbratilis* (Meek)
- **Phallichthys amates* (Miller)
- *Phallichthys tico* Bussing
- *Poecilia gillii* (Kner & Steindachner)
- **Poecilia* cf *sphenops* Valenciennes
- *Poecilia* sp.
- **Poeciliopsis gracilis* (Heckel)
- **Priapichthys annectens* (Regan)

Cichlidae "Mojarras, Guapotes"
- **Cichlasoma alfari* Meek
- *Cichlasoma centrarchus* (Gill & Bransford)
- *Cichlasoma citrinellum* (Günther)
- **Cichlasoma friedrichsthalii* (Heckel)
- *Cichlasoma labiatum* (Günther)
- *Cichlasoma longimanus* (Günther)
- *Cichlasoma maculicauda* Regan
- *Cichlasoma managuense* (Günther)
- *Cichlasoma nicaraguense* (Günther)
- *Cichlasoma nigrofasciatum* (Günther)
- *Cichlasoma rostratum* (Gill & Bransford)
- **Cichlasoma septemfasciatum* Regan
- **Cichlasoma tuba* Meek
- *Herotilapia multispinosa* (Günther)
- *Neetroplus nematopus* (Günther)

Synbranchidae "Anguilas"
- *Synbranchus marmoratus* Bloch

Species With Marine Affinities

Carcharhinidae "Tiburones"
- *Carcharhinus leucas* (Müller & Henle)

Pristidae "Peces Sierra"
- *Pristis pectinatus* Latham
- *Pristis perotteti* Müller & Henle

Megalopidae
- *Megalops atlanticus* Valenciennes

Clupeidae "Sabaletes"
- *Dorosoma chavesi* Meek

Atherinidae "Sardinas"
- *Melaniris sardina* Meek

Centropomidae "Robalos"
- *Centropomus parallelus* Poey

Pomadasyidae "Roncadores"
- *Pomadasys boucardi* (Steindachner)

Gobiidae "Guavinas"
- *Gobiomorus dormitor* Lacépède

[1]Incorrectly considered a synonym of *Cichlasoma spilurum* (Günther) by Meek (1914).

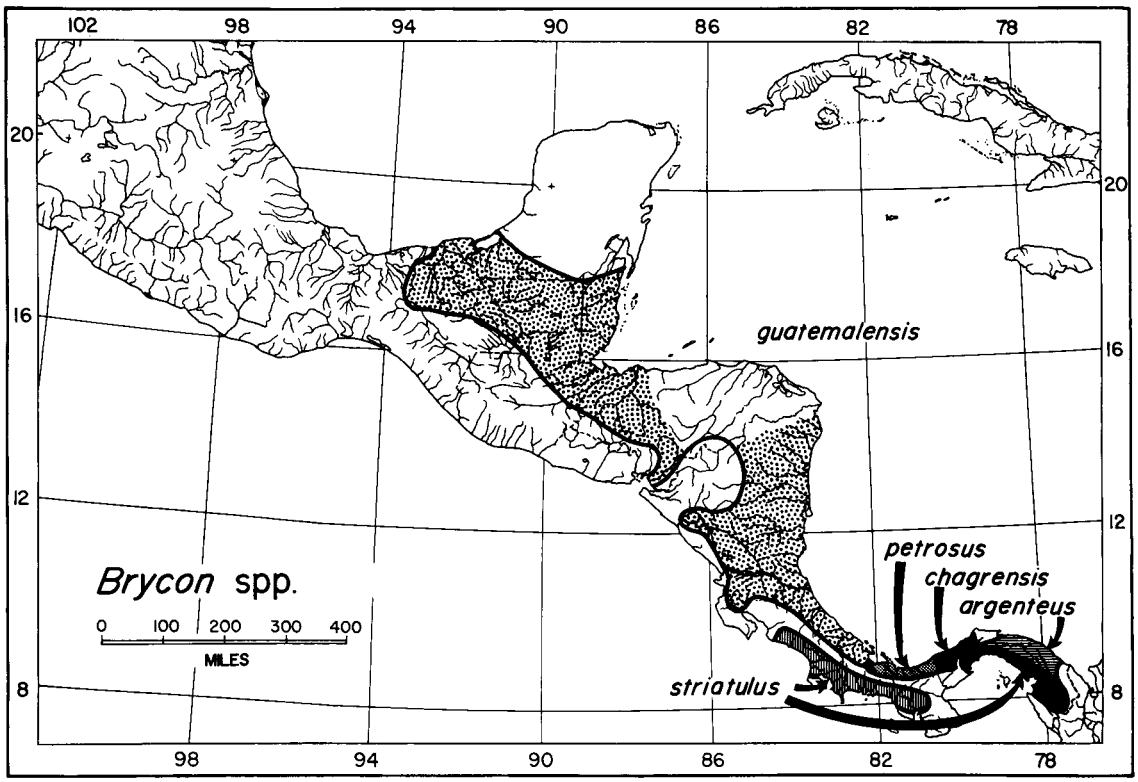

FIG. 3. Range of the genus *Brycon* in Central America. A member of the New Southern Element. This genus shows great differentiation in the isthmian region, but is represented by only one species north of Costa Rica. Two other nominal species of restricted range are not shown: *B. behreae* in western and *B. obscurus* in central Panamá. Negative evidence suggests a hiatus in the range of *B. guatemalensis* in eastern Honduras; northern limits have been estimated. Modified after Loftin (1965), Martin (1972) and Miller (1966).

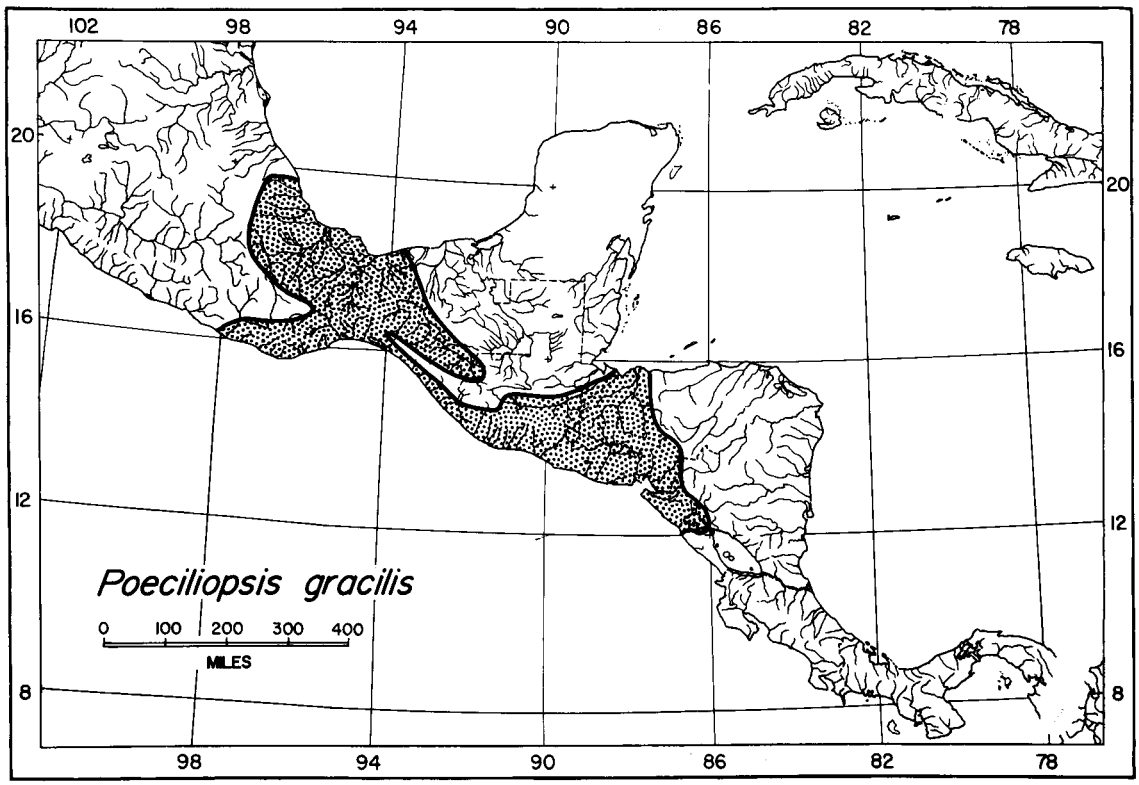

FIG. 4. Range of *Poeciliopsis gracilis*. This member of the Old Southern Element has an exceptionally wide Pacific distribution, and is also found at three Atlantic slope areas. Conversely to *Lepisosteus tropicus*, *P. gracilis* probably arose on the Pacific slope and later invaded the Atlantic versant. After Rosen and Bailey (1963), Miller (1966) and Villa (1971).

of the catfishes, it is possible that these species cannot compete with lake-adapted forms, especially those that are closely related. Where they are sympatric, *C. septemfasciatum* frequently dominates a sibling species, *C. nigrofasciatum*, in moving waters and apparently excludes it from some Costa Rican lakes. Near the coast however, the situation seems to be reversed (Gilbert and Kelso, 1971). *C. nigrofasciatum* is a prominent form in many Central American lakes of the Pacific slope where *C. septemfasciatum* does not occur. The combined success of *C. nigrofasciatum* and another close relative, *C. centrarchus*, may prevent *C. septemfasciatum* from establishing itself in Lake Nicaragua (Bussing, in prep.).

Cichlasoma alfari is common in many streams and rivers from Honduras to Panamá and also inhabits lakes in Costa Rica. Four fishes of the same species group of *Cichlasoma–C. longimanus, C. rostratum, C. citrinellum* and *C. labiatum*–perhaps combine to outcompete this species in Lake Nicaragua. Another species, *Cichlasoma friedrichsthalii*, is commonest in small standing waters or sluggish backwaters of large rivers. It and members of three other families (Table 2), *Bryconamericus scleroparius, Gymnotus cylindricus* and *Rivulus isthmensis* are found in lake affluents and are probably swept into the lake on occasions.

Six species have never been collected outside of the Great Lakes and are evidently autochthonous: *Astyanax nasutus, Rhamdia managuensis, R. barbata, Rhamdia* sp., *Dorosoma chavesi* and *Melaniris sardina. Cichlasoma labiatum*, probably another autochthonous species, is principally a lake form, but individuals have been collected in the Río San Juan. Several other species are restricted to watersheds adjacent to, or near the Río San Juan.

The San Juan Environment

West (1964) has summarized the major physiographic features and Tamayo and West (1964) the hydrography of Central America. Central Nicaragua is mountainous, but its broad lowland (Mosquito Coast) forms one of the most extensive coastal plains of Middle America. To the north in Honduras the Río Patuca and Río Coco have created immense deltas. South of the Coco delta, shorter rivers such as the Prinzapolka, Grande de Matagalpa and Escondido flow gradually to the sea, and in conjunction with longshore currents, have formed a series of sand bars, beach ridges and lagoons. The coastal plain tapers to a narrow strip south of the Río Escondido, Nicaragua, where the Cordillera de Yolaina approaches the sea. These coastal hills apparently constitute a filter-barrier to fishes living to the north or south of it. The Río San Juan drains the two Great Lakes of Nicaragua that occupy the Nicaraguan Depression. A considerable portion of northern Costa Rica is drained by tributaries that add to the San Juan discharge. Below the large San Juan delta in Costa Rica, short but voluminous rivers—such as the Río Chirripó, Parismina, and Matina —drain the narrowing coastal plain. Behind Punta Cahuita, the Fila Carbón reaches nearly to the sea, and has a significant filter-barrier effect, as shown by the computer analysis, between the Matina and Sixaola drainages. South of the Río Sixaola and Changuinola in Panamá, the coast is mountainous and the slopes are drained by a series of short streams.

Total annual precipitation and seasonal distribution of rainfall play an important role in fish distribution. The rain fall pattern in the San Juan Province is extremely patchy. Mean annual precipitation ranges from less than 1000 mm in central Nicaragua to over 6000 mm at the mouth of the Río San Juan (Vivó, 1964). Rainfall is greatest near the coast, but still varies between about 2000 to over 6000 mm per year. The relatively low precipitation over much of the Nicaraguan sector may partially explain the paucity of freshwater fishes in the region.

Ecologic Considerations

Lake Nicaragua is oval in shape, 165 km long by 75 km wide and has an area of 8,264 km^2. Estimated average depth is between 12 and 20 meters; the greatest depth recorded during the recent INFONAC (1973) survey was 20 fathoms (36.5 meters). The bottom is principally mud, but sand occurs near the northern and western shores and rocks appear frequently in deep areas.

Most of the following observations are based on experimental trawling in the northern sector of Lake Nicaragua between 25 and 30 November 1971 by the INFONAC vessel M/N Gaspar. Fishing gear for this preliminary cruise consisted of a 2 meter try-net, gill nets, and seines. Ichthyocide was used to advantage on one occasion. Subsequent systematic trawling over the entire lake bears out the earlier data with respect to vertical distribution, but reveals that most fishes are also limited horizontally by the nature of the substrate or other factors (INFONAC, 1973).

Cichlids are the most abundant bottom fish in depths up to about 10 meters. A few *Cichlasoma longimanus, C. centrarchus* and *C. nicaraguense* were present in the deepest (15 meters) haul made. Baylis (1973) observed that cichlids in Laguna de Xiloá, Nicaragua were present but scarce below 25 meters. *Cichlasoma rostratum* was most common over debris near the mouths of rivers. *C. nigrofasciatum, Herotilapia multispinosa* and the large-mouthed *Guapotes* (*Parapetenia* species group) were taken only close to shore. We collected only normal-colored (brown) *C. citrinellum*, but fishermen reported that rubric forms of both it and *C. labiatum* are most abundant over rocky bottom and in other areas of the lake.

Several specimens of *Astyanax nasutus* were taken in the try-net in spite of its large mesh. On one occasion a school was seen on the surface over deep water. The appearance of netted specimens suggests they probably occur near the bottom, and possibly throughout the water column. *A. nasutus* were seined off sandy beaches, but were replaced entirely by *A. fasciatus* in the mud-bottomed inner reaches of "esteros". The planktonivorous *A. nasutus* averages 29.1 total gill rakers vs. 24.0 for *A. fasciatus*. Apparent hybrids between *A. fasciatus* and *A. nasutus* were rare.

A case of incipient speciation is worthy of note. Lacustrine *A. fasciatus* exhibit an extreme variation in number of maxillary teeth: 2-9 teeth on each maxillary, $\bar{x} = 4.5$ vs. 1-5 teeth, $\bar{x} = 2.2$ for specimens inhabiting tributaries of the lake. Eigenmann and Ogle (1907) proposed the name *Astyanax rutilus nicaraguensis* for this form, which Eigenmann (1921) later changed to *A. nicaraguensis*.

Poecilia gillii and *Poecilia* sp. were observed and collected only in shallow water. Several large slim specimens, presumably *Poecilia* sp., were once observed on the surface about 50 meters from shore in an "estero". *Poecilia* cf *sphenops* has been taken only in tributaries of the lake (Astorqui, 1972).

The catfish, *Rhamdia* was most abundant in water deeper than 10 meters. *Rhamdia* sp. only occurred in the deepest hauls (12-15 meters) and was replaced by *R. barbata* in shallower water (1.5-12 meters). The deepest collections surprisingly revealed *Hyphessobrycon tortuguerae* (2 specimens), *Synbranchus marmoratus* (5 specimens) and *Neoheterandria*

umbratilis (10 specimens). All of these species had little pigmentation and one *Synbranchus* was entirely colorless. It is likely that the latter two species were collected near the bottom, although *H. tortuguerae* may have been taken at any depth. Large bivalves were common in some of the deepest hauls.

For purposes of later discussion, some ecologic traits of the sections or subgenera of *Cichlasoma* as recognized by Regan (1905: 1906–08) and modified by Miller (1966) and Bussing and Martin (1974) are presented:

1) Section *Theraps*— the many species of this section and its specialized offshoots *Paraneetroplus* and *Neetroplus* are moderate-sized herbivores. This group is not known to have an affinity with any extant South American cichlids.

2) Section *Archocentrus*— a few small insectivores, although the derived *Herotilapia multispinosa* is an algivore. On the basis of general morphology, other than tooth profile, *Herotilapia* appears to be a cognate species of a lineage including *Cichlasoma centrarchus* and *C. spinosissimum*. Regan (1905) stated that the group was probably derived from the same ancestors as the South American species *Cichlasoma facetum*.

3) Section *Amphilophus*— a group of moderate-sized forms which are to large degree detritus feeders. Bussing and Martin (1974) have suggested that this group gave rise to the distinctive northern Middle American section *Thorichthys* which is not represented in the region under consideration. Regan (1905) noted that these forms resemble the South American *Cichlasoma bimaculatum* in their generalized dentition.

4) Section *Parapetenia*— small to large carnivores with large canine teeth and greatly protractile jaws. Members of this species group also occur on the Antilles and in South America. Regan (1906–08) mentioned two lineages and their possible Central and South American representatives. *Petenia splendida* is probably a derivative of this section which has developed in the Usumacinta Province.

Zoogeographic Considerations

Paleogeography.— Of special interest to the present discussion is the status of southern Middle America during Cenozoic times. Vinson and Brineman (1963) mentioned a major hiatus in Paleocene deposits which implies a general uplift of the region after the end of the Cretaceous. This scarcity of Early Tertiary formations suggests a land bridge connecting Central America and South America during Paleocene time (Fig. 5). According to Lloyd such a connection emerged for the first time in geologic history in the Pliocene.

Dengo (1962a, 1968) and Lloyd (1963) have suggested that the Isthmian Link (lower Central America) had its origin as a submarine promontory in the Pacific. On this promontory a series of volcanic islands formed an archipelago (Fig. 5) between Nuclear Central America and South America (Dengo, 1968). This arc perhaps formed in the Cretaceous. Parts of such an arc were figured by Lloyd (1963) as still emergent in Eocene-Oligocene times. Dengo (1962b) presented evidence that much of northwestern Costa Rica (called Guanarivas by Lloyd, 1963) has remained emergent since Cretaceous. The present peninsulas of Nicoya, Osa and Azuero, which have been emergent throughout the Cenozoic (Fig. 6) may also represent part of this same archipelago (Dengo, 1968). The presence of Miocene mammals of North American affinity in the Panama Canal Zone suggests that this tectonically active archipelago to the west and north of the isthmian region was in considerable contact with North America (Fig. 7) throughout the Tertiary (Vinson and Brineman, 1963).

Renewed tectonic activity in Eocene (Dengo, 1962a) or Oligocene times (Lloyd, 1963) produced the Talamancan Cordillera which emerged first as a series of islands in present day southern Costa Rica and western Panamá. This second island chain lay slightly northward of the earlier archipelago and was destined to form the present backbone of Central America. By Miocene age the Talamanca-Tabasará emergence was completed to form an extensive island (Fig. 6). Lloyd (1963) considered eastern Panamá geologically different from the Isthmian Link and called it the Panamá Spur, but Dengo (1968) indicated that all of the isthmian region had a similar geologic history. Whitmore and Stewart (1965) refuted the Panamá Spur concept and felt that the Bolivar Trough prevented connection of eastern Panamá with South America until very Late Tertiary (Fig. 7). They designated the region the San Blas Area (Fig. 6) and believed that it was an island at least in Early and Late Miocene times. Similar Middle Tertiary islands are proposed for the lower Central American region by Maldonado-Koerdell (1964).

The Nicaraguan Depression was depicted as a transcontinental trough during most of Tertiary (Fig. 6) until Late Miocene or perhaps Pliocene times by Lloyd (1963) and Vinson and Brineman (1963). Whitmore and Stewart (1965) admitted that such a trough may have existed during part of Miocene time and that mammal migration could have occurred in several stages across short-lived water barriers in southern Central America.

The Amatique embayment region, the eastern portion of the former Chapayal seaway which cut across Chiapas, southern Petén and southern British Honduras, was a large inland arm of the sea lying over the present day Río Polochíc and Río Motagua drainages of Guatemala (Vinson and Brineman, 1963). The Chapayal Basin was interrupted in early Miocene, but the Amatique basin persisted until Pliocene times.

Dengo (1968) described another marine embayment, the Mosquitia basin, which encroached on northeastern Honduras and Nicaragua during Eocene-Pliocene times (Figs. 6 and 7).

In the Pliocene, uplift along the present axis of Central America including the Talamanca and San Blas Islands, resulted in a land bridge between the American continents (Lloyd, 1963; Maldonado-Koerdell, 1964; Dengo, 1968). The Nicaraguan Depression perhaps remained an inland sea connected to the Caribbean (Lloyd, 1963). Wilson and Auer (1942), Zoppis and del Giudice (1958), and Swain (1961) believed that the Great Lakes were never connected with either ocean, but that the depression is a graben formed in Late Tertiary and Quaternary, which subsequently filled with runoff to form lakes.

An older opinion by Hayes (1899) proposed that part of the Great Lakes basin was derived from a large bay of the Pacific Ocean, and was popular until recent years. He postulated that a Pacific bay covered present Lake Managua and the northwest corner of Lake Nicaragua in Late Tertiary. Volcanic activity in Late Pleistocene or Early Recent time gradually closed the bay, isolating it from the sea. Freshwater runoff caused the level to rise and it probably overflowed down the Pacific versant. Continued tectonic activity raised the outlet and the waters backed up to fill the entire depression to a level probably 15 meters (50 feet) or

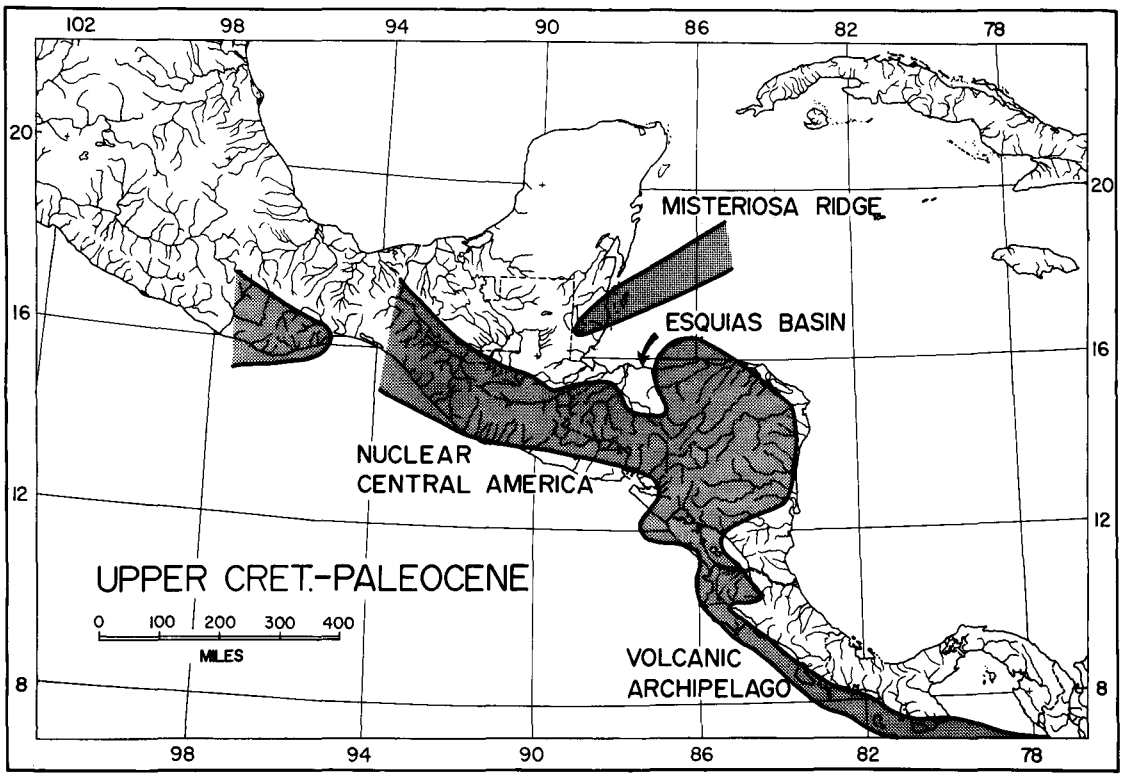

FIG. 5. Composite of some of the major features, not necessarily concurrent, of Central American Late Cretaceous or Paleocene geography. The volcanic archipelago connecting Nuclear and South America of Dengo (1968) is figured as a land bridge on the basis of biological evidence of an early arrival of South American fishes into Central America. Compiled from sources mentioned in the text.

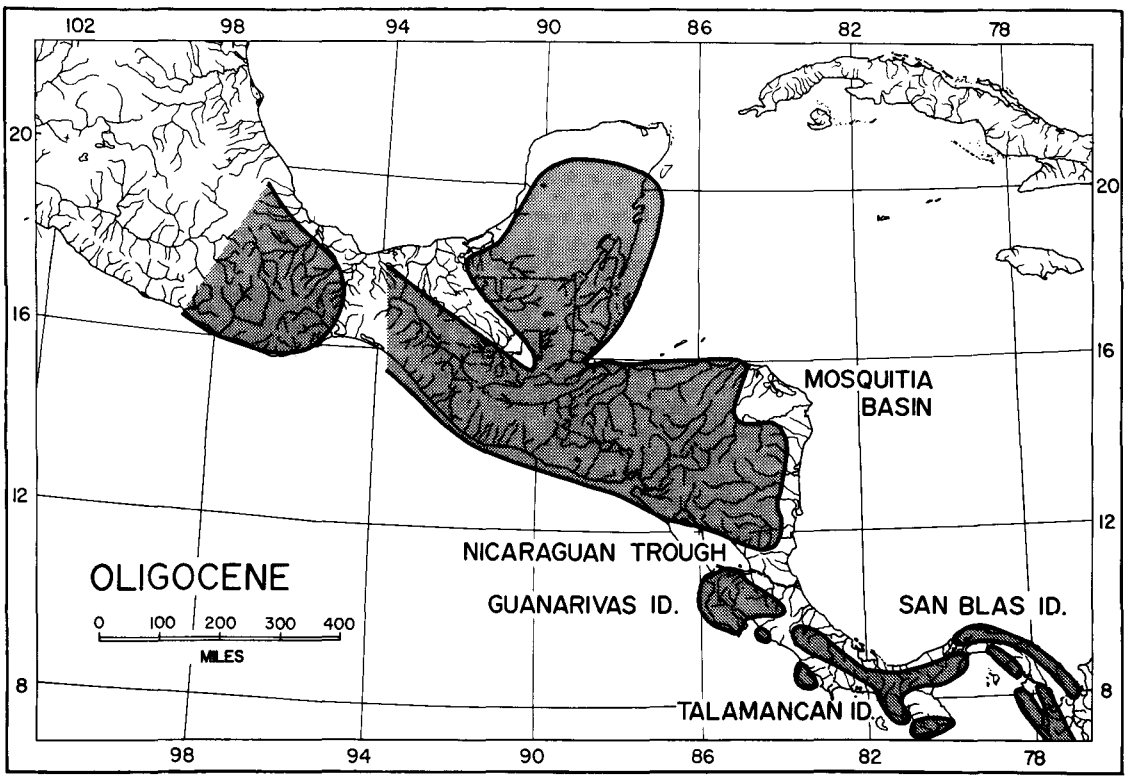

FIG. 6. Principal emergent Central American landmasses of Oligocene times. Compiled from geological works mentioned in the text.

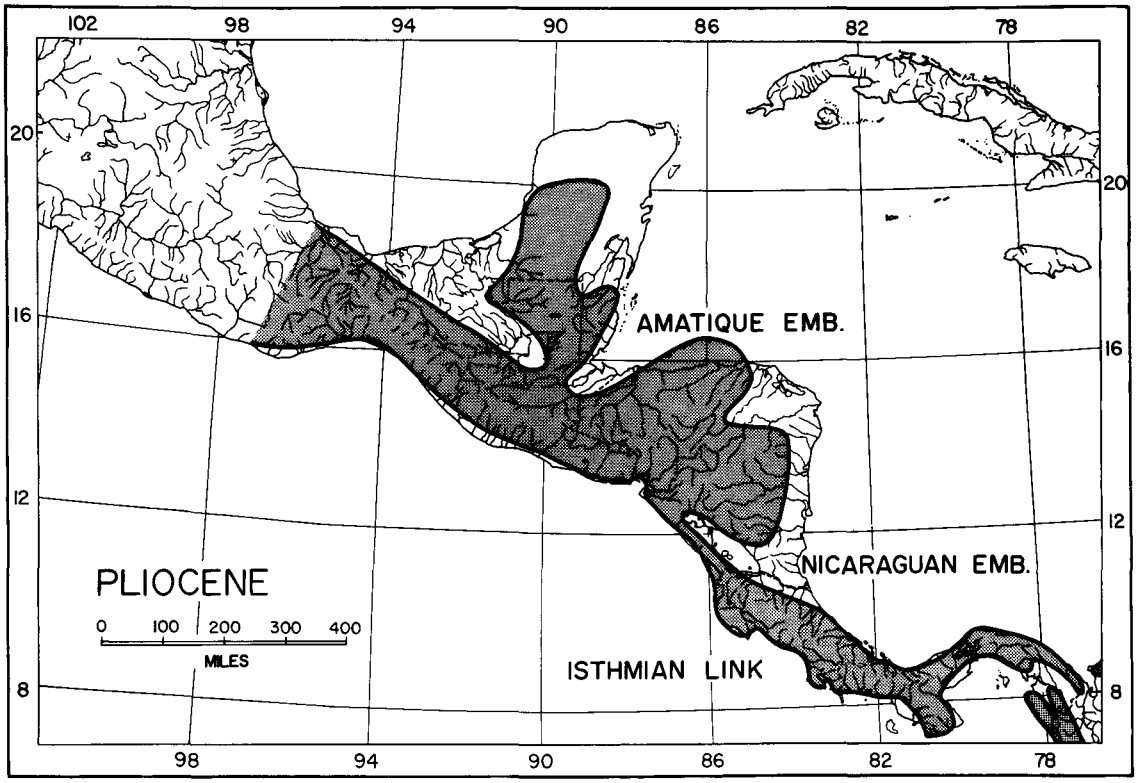

FIG. 7. Probable configuration of Central America in Pliocene times. Compiled from geological literature mentioned in the text.

more above the present level of Lake Nicaragua until it reached the Continental Divide, whereupon it flowed down the Atlantic slope. The resultant Río San Juan has cut away a channel until the present level of the lakes was reached. Tamayo and West (1964) related a different history for the Río San Juan: the upper portion of the river was once a former tributary of Lake Nicaragua which was later captured by the lower San Juan eroding headward from the Atlantic.

Villa (1968) proposed a synthesis of both major hypotheses. He accepted the tectonic origin of the depression, but favored a Pacific connection through the Golfo de Fonseca. Only sediment samples from throughout the depression will reveal the true history of the region. Thorson *et al.* (1966) discussed in some detail the theories of Pacific and Atlantic origin of the lakes. By the beginning of Pleistocene the present outline of Central America had been approximately delineated.

Aside from Costa Rican fossil cichlids from Pleistocene deposits, the only fossil material known from the Caribbean region is a single Miocene cichlid, *Cichlasoma woodringi* from Hispaniola. The species is very similar to its descendant *C. haitiensis* (*Parapetenia* species group), but has a lower vertebral count (Tee-Van, 1935). Both forms are quite similar to Central American *Parapetenia* group cichlids. Myers (1966) cited the lack of morphological diversity of Central American cichlids as evidence that their evolution has been rapid and of no great geologic age. On the basis of the Haitian fossil, he proposed an Early Miocene or earlier cichlid colonization in Central America. Although the degree of morphological differentiation within the family Cichlidae in Central America is not great, several species groups and three genera are presently recognized. Some of these endemic species groups of *Cichlasoma* are equivalent to genera in other fish families. In view of these facts and the slight degree of variation between the Middle or Upper Miocene *Cichlasoma woodringi* and the modern *C. haitiensis*, I feel it is quite reasonable to propose that cichlids and other members of an Old Southern Element reached Central America in Late Cretaceous or Paleocene times when the geologic evidence favors an intercontinental land bridge.

Aside from the minor clue to the evolutionary rate of cichlid fishes, we know nothing about rates of evolution in other groups and little about the selection pressures operating upon them. Thus, the possible chronologies of biologic events to be discussed are based heavily on the geologic evidence previously cited. An analysis of freshwater fish distribution in Central America corroborates the geologic evidence of the following outstanding Cenozoic events:

1) The presence of a land connection between Nuclear Central America and South America in Late Cretaceous or Paleocene times (Fig. 5).

2) The isolation of Central America from South America by the Bolivar Trough and probably other seaways between the Eocene and Pliocene (Fig. 6).

3) The continued emergence of Middle Tertiary landmasses south of the Nicaraguan Trough since the Late Cretaceous or Paleocene invasion of freshwater fishes (Fig. 6).

4) The presence of the Nicaraguan Trough acting as a barrier to freshwater fish dispersal on the Atlantic versant during Middle Tertiary and perhaps at other times (Fig. 6).

5) The persistence of the Amatique embayment as a filter barrier to freshwater fish dispersal from Early Miocene until Pliocene times (Fig. 7).

6) The presence of the Mosquitia embayment over much of the present Mosquitia lowland between the Eocene and Pliocene (Figs. 6 and 7).

7) The reconnection of the two continents by the closure of the Bolivar seaway in Pliocene time.

8) The drainage toward the Pacific of a former Great Lake of Nicaragua at some time when the lake was 15 to 20 meters higher than its present level. Either the origin of the Great Lakes basis as a graben or a marine embayment would account equally well for the present distribution of the freshwater fishes.

Some principles of biogeographic analysis.— In an earlier draft of this manuscript I analyzed the present distribution of families, genera and species of freshwater fishes in the San Juan Province. I gave considerable importance to the distribution of individual species in an effort to determine their centers of origin and attempted to explain their extant distributions by proposing dispersal routes and in some cases, invoking descent of monophyletic lineages from salt-tolerant ancestors. In two or three cases where several unrelated species had similar coincident distributions, considerable insight into their common histories was gained. This approach however, did not explain some important phenomena (*e.g.*, the relatively high diversity of species in the San Juan drainage and the apparent paucity of endemic species in the Honduran-Nicaraguan region).

Dr. Donn E. Rosen kindly allowed me to read parts of two manuscripts (Rosen, 1974; Croizat, Nelson and Rosen, 1974; see Nelson, 1973 for further pertinent discussion) which discuss and apply an alternative approach to zoogeographic analysis. This approach maintains that there are two kinds of distribution patterns. One, which appears to be fundamental to all patterns of distribution, is the result of the subdivision *in situ* of an ancestral species into descendent species as a consequence of past geographic changes. Ancestral patterns are reflected by the present distribution of a monophyletic group such as a family, genus or species. Superimposed on such primary patterns are secondary patterns which are a result of subsequent dispersal. Thus, sympatry within a monophyletic group suggests active migration if the allopatric speciation model is accepted.

On the basis of the above criteria, I find that in lower Central America many generic distributions appear to approximate the distributions of formerly widespread ancestral species. Within other genera (*i.e.*, *Cichlasoma*, *Brachyrhaphis, Poecilia* and probably *Rhamdia*) two or more monophyletic lines are apparent, each of which contains several species which have more or less allopatric but contiguous distributions.

Considered below are the distributions of monophyletic groups, the reasons for their subsequent subdivision into descendent forms, and the ensuing events which permitted dispersal and sympatry between closely related species. Variables such as salt tolerance and rate of evolutionary change of different groups of fishes are discussed, but not employed in reconstructing chronologies of past events.

Primary Patterns.— Two basic ancestral distributions of monophyletic groups are evident in the San Juan Province. Most genera and species groups that conform to these patterns are assumed to have had similar histories and are, of course, just a part of a much larger Central American biota which has been affected by similar past events.

Savage (1966), in treating the Central American herpetofauna, applied the term Element (subdivided into Complexes and Components) to groups of genera with similar historical distribution patterns. I use these terms in a similar historical connotation, but use a somewhat different nomenclature to refer to ichthyological units. The principal ancestral patterns are:

1. Old Southern Element.—most freshwater fishes in the San Juan Province form part of this tropical element which has developed mainly on the Atlantic versant. Several of these lineages are endemic to the area, but have South American affinities, *e.g., Phallichthys, Alfaro, Brachyrhaphis, Gambusia, Belonesox* (Fig. 8), and several species groups of *Cichlasoma*). Other genera belonging to this element are widely distributed in South America as well, but their species complements are endemic to Central America and the Antilles (*e.g., Hyphessobrycon* (Fig. 9), *Gymnotus,* and *Rivulus*). The genus *Rhamdia,* or species groups of *Rhamdia,* appear to have similar distributions to other lineages that make up this element, but confirmation of this must await further study.

Nearly all groups comprising this element range from extreme western Panamá to southern México and have been largely confined to the Atlantic versant. Many are not represented south of Costa Rica. On the basis of geologic evidence, it appears that this element first reached Middle America in Late Cretaceous or Early Tertiary times.

2. New Southern Element.— A few genera that have reached the San Juan Province occur on both versants, at least in lower Central America. With the exception of *Bramocharax,* the genera comprising this tropical element are all found in South America, where many are widely distributed (*e.g., Astyanax, Brycon* (Fig. 3), *Bryconamericus, Roeboides, Carlana,* and *Synbranchus*). The northern limit of each of these genera varies considerably— to as far north as southern United States or only to northern Nicaragua. Each group is represented by several species in the isthmian region, but usually by only one form further north. Numerous other genera which do not extend north of Panamá also belong to this element. It will be shown that these stocks reached Central America from the south in Pliocene times.

Five other genera represented in the San Juan Province do not conform to these basic distribution patterns. The genus *Lepisosteus* (Fig. 2) undoubtedly represents a northern or temperate element which reaches its southern limit in northern Costa Rica. On the Atlantic slope *Lepisosteus tropicus* reaches southern México and Guatemala and the Río San Juan drainage of Nicaragua and Costa Rica, but has not been reported in the intermediate region. On the Pacific slope it reaches the Golfo de Fonseca. The genus *Poeciliopsis* was derived from the Old Southern Element and is almost entirely restricted to the Pacific versant of México, Middle America and part of Colombia. *Poeciliopsis gracilis* (Fig. 4) is found on the western slope from Oaxaca, México to the Golfo de Fonesca; it also occurs on the eastern slope from southern México to western Honduras and reappears further south in the Río San Juan drainage. The similar distributions of *Lepisosteus* and *P. gracilis*, each with disjunct populations in the Río San Juan, suggest that these representatives of different historical elements, nevertheless, have had more recent similar histories probably during most of the Tertiary.

Before mentioning the present distributions of the other three species, it is important to point out that in order to obtain the earliest picture of poeciliid evolution in Central America, it is best to consider as ancestral lineages, tribes rather than genera. If the genera of each tribe are plotted

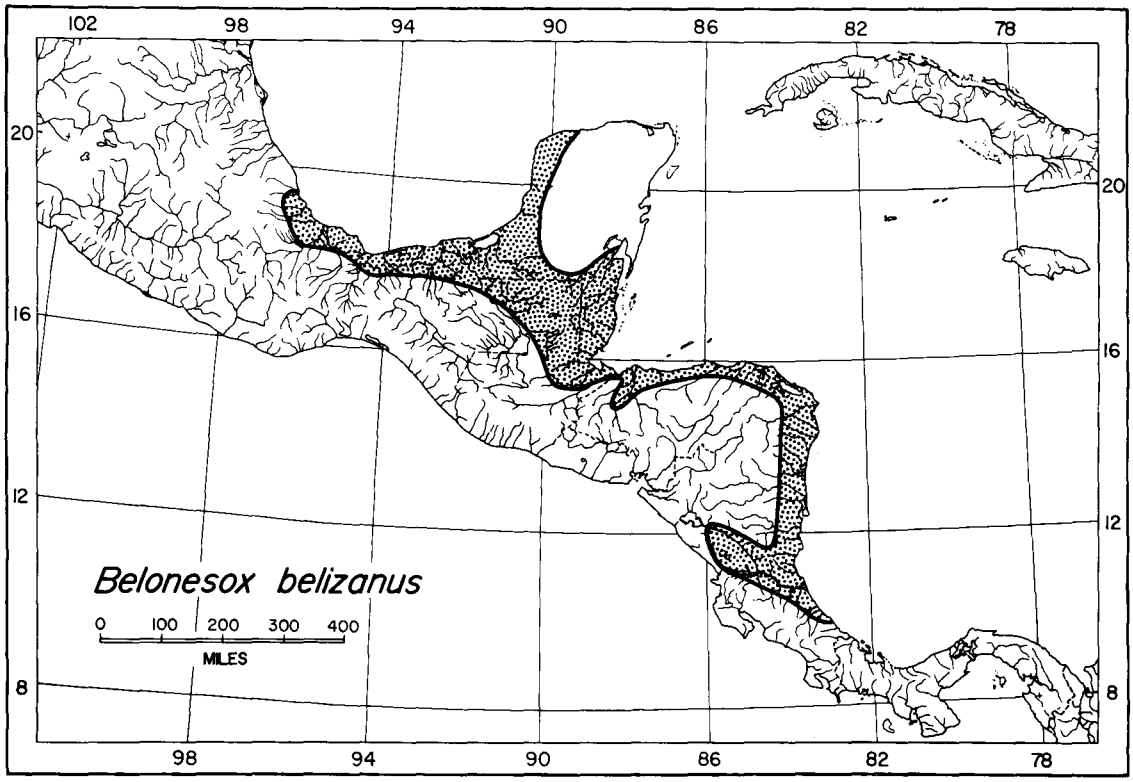

FIG. 8. Range of *Belonesox belizanus*. An example of a salt-tolerant species of the Old Southern Element which did not differentiate into other forms in the Upper Tertiary.

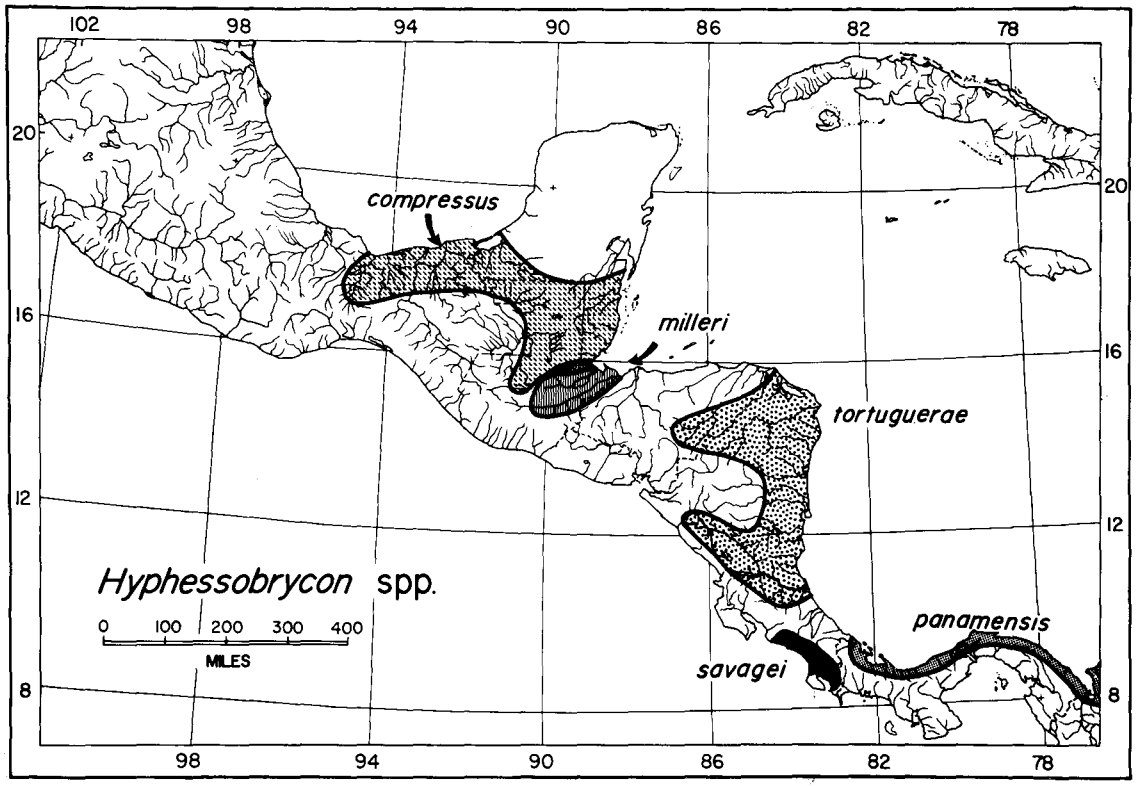

FIG. 9. Range of the genus *Hyphessobrycon*. An example of the complementary distribution of the species of this Old Southern lineage in Central America. Western and Eastern Nuclear Central American Complexes and Atlantic and Pacific Components of the Talamancan Complex are represented by *H. milleri, tortuguerae, panamensis* and *savagei* respectively. Modified after Loftin (1965), Martin (1972) and Miller (1966).

on a map, the resultant, often complementary patterns appear to reveal an older distribution of one or two lineages within each tribe. Three tribes have reached far north into the Temperate Zone, and representatives of each (*e.g., Poecilia, Gambusia* and *Heterandria*) have probably arisen north of Middle America and been subject to early subdivisions which are beyond the scope of this study.

The *Mollienesia* species group of *Poecilia* was probably derived from the Old Southern Element, but has developed farther north than most other groups of the element and occurs on both versants and the West Indies. Speciation has been most extensive in northern Middle America and only two forms are recognized in Panamá.

Two other poeciliid genera, *Priapichthys* and *Neoheterandria*, are confined to lower Central America and northwestern South America and represent the southernmost segment of the tribe of Heterandriini. Except for *P. annectens*, other *Priapichthys* are found only on the Pacific slope. Species of *Neoheterandria* occur on both versants.

Thus, an early freshwater fauna of southern origin originally populated the entire Atlantic versant of Central America and has been largely confined to that versant until present time. A younger southern ichthyofauna subsequently has inhabited both slopes in lower Central America and has extended northward to a variable extent along both versants. Only one derivative of a northern element reaches the area under consideration (Table 3).

Subdivision of major elements.— It is necessary now to examine the major subdivisions of the historical elements. If many genera or species groups of an element are similarly subdivided, this in turn supports the assumption that the members of the same element have shared similar histories. Once these subdivisions have been delineated, a physiogeographic explanation is in order.

A striking pattern of subdivision of the Old Southern Element overshadows all others in Central America. Numerous groups are represented by cognate species whose principal distributions lie on the Atlantic versant at three cardinal centers: 1) present day southern México-Guatemala, 2) Honduras-Nicaragua, and 3) Costa Rica-western Panamá (Fig. 9). These three regions are hereafter referred to as the Western Nuclear Central American, Eastern Nuclear Central American and Talamancan Complexes (Table 4). The Talamancan Complex in turn contains an Atlantic and a Pacific Component. Further study will probably reveal the merit of likewise considering the Eastern Nuclear Central American Complex as comprising Honduran and Nicaraguan Components.

TABLE 3. Component genera of historical assemblages of the Central American ichthyofauna which reach the San Juan Fish Province.

Old Southern Element	New Southern Element
Hyphessobrycon	*Astyanax*
Gymnotus	*Bramocharax*
?Rhamdia	*Brycon*
Rivulus	*Bryconamericus*
Alfaro	*Carlana*
Belonesox	*Roeboides*
Brachyrhaphis	*Synbranchus*
Gambusia	
Neoheterandria	Northern Element
Phallichthys	*Lepisosteus*
Poecilia	
Poeciliopsis	
Cichlasoma	
Herotilapia	
Neetroplus	

A glance at a map of Pliocene geography (Fig. 7) reveals how the Amatique embayment nearly split Nuclear Central America into western and eastern segments. Likewise the Nicaraguan Trough (Fig. 6) and perhaps to a certain extent later, the Nicaraguan embayment (Fig. 7) effectively isolated Eastern Nuclear Central America from the Talamancan landmass to the south.

The steep and faulted southern face of the Amatique embayment (Vinson and Brineman, 1963) probably provided only for short precipitous drainage basins which greatly inhibited the dispersal of freshwater fishes. The Nicaraguan Trough was an absolute barrier to freshwater fish dispersal; later, the Nicaragua embayment was probably also flanked by mountains with relatively short drainage patterns, which apparently impeded passage of freshwater fish around the embayment.

The Mosquitia basin has had a filter barrier effect within the Eastern Nuclear Central American Complex. The result of this effect however, seems not to have caused a differentiation within the complex, but to have restricted movement into the Honduran Component. Several species are represented in the Nicaraguan Component, that do not appear in or barely reach Honduras: *Hyphessobrycon tortuguerae, Rivulus isthmensis, Brachyrhaphis holdridgei, Herotilapia multispinosa,* and *Cichlasoma alfari*. Only *Alfaro huberi* and *A. cultratus* may have differentiated from common stock as a result of the Mosquitia basin filter barrier.

The relatively diverse ichthyofauna which comprised the

TABLE 4. Some lineages of the Old Southern Element and their probable descendent cognate species.

	Nuclear Central American Complexes		Talamancan Complex	
	Western	Eastern	Atlantic Component	Pacific Component
Hyphessobrycon	*milleri*	*tortuguerae*	*panamensis*	*savagei*
Gymnotus	sp.	*cylindricus*		
Rivulus	*godmani*	*isthmensis*	sp.	*hildebrandi*
Alfaro		*huberi*	*cultratus*	
Brachyrhaphis		*holdridgei*	*parismina*	?
Phallichthys	*fairweatheri*	*amates*	*tico*	
Poecilia	*mexicanus*	sp.	*gillii*	*gillii*
Cichlasoma				
(Amphilophus)	*robertsoni*	*longimanus*	*rostratum*	
(Archocentrus)	*spilurum*	*nigrofasciatum*	*septemfasciatum*	*sajica*
(Archocentrus)	*spinosissimum*	*H. multispinosa*	*centrarchus*	
(Parapetenia)	*multifasciatum*	*friedrichsthalii*	*friedrichsthalii*	
(Parapetenia)	*motaguense*	*dovii*	*managuense*	
Neetroplus	*P. bulleri*		*nematopus*	

Atlantic Talamancan Component clearly suggests the continued emergence of a landmass in southern Central America, at least since Middle Tertiary (*i.e.*, sometime before the Nicaraguan Depression was a transcontinental trough). This supports Whitmore and Stewart's (1965) contention that ". . . by early middle Miocene time, extensive emergence had connected nuclear Central America with the area of the present Canal Zone".

Three derivatives, presumably of the Old Southern Element (*Cichlasoma maculicauda, Belonesox belizanus* and *Gambusia nicaraguensis*), occur along most of the Atlantic slope of Central America near the coast or in brackish or sometimes marine biotopes. These forms have not developed distinct descendent species in each of the components as have many of the other Old Southern derivatives. These species may have entered the area subsequent to the dissapearance of the marine embayments, but it is quite possible that populations of these salt-tolerant forms were present in the region, but not isolated as were truly freshwater fishes. Thus, differentiation would not have taken place.

Another recurrent pattern of subdivision involves descendants of a common Talmancan ichthyofauna. As the insular Talamancan Cordillera emergence accelerated in Late Miocene and Pliocene times (compare Figs. 6 and 7), it became reconnected with Nuclear Central America and the Isthmian Link (Dengo, 1968), thus permanently subdividing the Atlantic and Pacific populations. Four cichlids with present ranges centering around the San Juan drainage have cognate forms on the Pacific versant of southeastern Costa Rica. Although now separated by the Continental Divide, each of these species pairs is probably derived from a common Talamancan ancestor. These Trans-American geminate pairs are (representatives of Atlantic and Pacific Components respectively): *Cichlasoma alfari* and *C. diquis*; *C. citrinellum* and *C. lyonsi*; *C. tuba* and *C. sieboldii*; and *C. septemfasciatum* and *C. sajica*. The Atlantic Talamancan derivative, *Hyphessobrycon panamensis* and Pacific Costa Rican *H. savagei* are more similar to each other than either is to *H. tortuguerae*, an Eastern Nuclear Central American derivative (Fig. 9). It is thus likely that *H. savagei* is the Pacific Talamancan derivative of this geminate pair. Similarly, *Rivulus hildebrandi* of southeastern Costa Rica appears to be closely related to *R. isthmensis* and *R. godmani* (Table 4) of the Atlantic versant, and is the Pacific Talamancan geminate of an undescribed form of the Atlantic versant of Costa Rica. Species of the poorly known genera *Rhamdia* and *Brachyrhaphis* may also be shown to have geminate derivatives of the Talamancan Component.

At the California Academy of Sciences I have examined part of the collections made by Ellinor Behre (1928) on the Atlantic slope of western Panamá. Cichlids identified by her both as *C. altifrons* and *C. calobrense* appear to represent the same species and may well represent the latter form, formerly known only from the Río Bayano and Tuira basins of eastern Panamá. Regardless of its identity, Behre's material, although clearly distinctive, appears to be closely related to *C. altifrons* of the Pacific slope of southeastern Costa Rica and western Panamá. These may prove to represent yet another geminate species pair of Talamancan descendants.

The genera *Priapichthys* and *Neoheterandria* have speciated in the isthmian region much as have members of the New Southern Element, and they also occur in South America. On the other hand, these lineages, although closely related to each other, are not markedly different from other heterandrin genera (Rosen and Bailey, 1963), such as one would expect if they had been separated from them during much of the Tertiary. On the basis of this lack of any sharp division in the tribe Heterandriini, I think it is best to consider *Priapichthys* and *Neoheterandria* part of the Old Southern Element.

Only a few of the New Southern lineages are considered here, because so few reach the San Juan Province. Four important genera—*Astyanax, Brycon* (Fig. 3), *Bryconamericus* and *Roeboides*— reveal considerable subdivision and resultant differentiation of the ancestral stock in the isthmian region. North of Costa Rica each is represented by only one species. A combination of subdivision of the isthmian region in Pliocene-Pleistocene times and a late closing of the Nicaraguan embayment could account for this species diversity pattern if isthmian populations were prevented until the Late Pliocene or Pleistocene from overcoming the Nicaraguan embayment filter-barrier and were concurrently subdivided by climatic or geographic events. The alternate rise and drop in sea level during the glacial ages of the Pleistocene may have played a role in this subdivision. The species distributions of the New Southern genera *Astyanax, Brycon* (Fig. 3), *Bryconamericus, Roeboides, Cheirodon, Gephyrocharax* and the Old Southern genera *Brachyrhaphis, Rivulus, Priapichthys* and *Neoheterandria* suggest that at least three isthmian sites were partially isolated from one another: present day southeastern Costa Rica, western Panamá and eastern Panamá.

Unlike other species groups of the New Southern Element, the *Astyanax fasciatus* species complex and the genus *Synbranchus* have reached the southern United States and southern México respectively. In spite of this extensive distribution, neither has been subject to considerable subdivision. The ancestral *Astyanax* has differentiated into perhaps two or three species in the isthmian region and *A. nasutus* in the Great Lakes. *Synbranchus* probably gave rise to the Yucatán cave species, *Furmastix infernalis*.

Bramocharax has differentiated into two species in Guatemala, one of which is represented by a disjunct population in the Río San Juan drainage (Rosen, 1972). The xeric climate of parts of Honduras-Nicaragua and marine inundations of much of the region until the Pliocene may be responsible for this hiatus as well as the general impoverishment of the region.

Carlana presently occurs in the Río San Juan drainage and Atlantic watershed of Costa Rica, and in Colombia and western Ecuador. This lineage was apparently unable to by-pass the Nicaraguan embayment and later, probably due to climatic changes, was eliminated from the isthmian region.

Secondary patterns and dispersal.— Sympatry of cognate species is considered evidence of dispersal subsequent to the disappearance of barriers which earlier permitted differentiation. Descendants of the Western and Eastern Nuclear Central American and Talamancan Complexes have dispersed to the north and south on the Atlantic slope and several have crossed the divide to the Pacific side. The closure of the Amatique and Nicaraguan embayments perhaps in Pliocene and Pleistocene times respectively, permitted interactions between faunas long separated. Due to the physiological nature of freshwater organisms, freshwater fish dispersal since these filter-barriers disappeared has not been extensive, nor has it been unidirectional. Movement of the descendent species of each lineage seems to have been determined by complex physical and biological interactions.

The only striking secondary distribution pattern is the concentration of species of Eastern Nuclear Central American and Atlantic Talamancan origins in the Río San Juan watershed. The two cognate components have merged precisely at this point and the interactions between them has resulted in sympatry (*e.g., Cichlasoma longimanus* and *C. rostratum; C. nigrofasciatum* and *septemfasciatum; Herotilapia multispinosa* and *C. centrarchus; Phallichthys amates* and *P. tico;* and *Brachyrhaphis holdridgei* and *B. parismina*) or progressive replacement of one species by its cognate (*e.g., Hyphessobrycon tortuguerae* replacing *H. panamensis*, Table 4 and Fig. 9). In other cases one or the other cognate had presumably retreated before any contact was made (*e.g., Rivulus isthmensis* and *Rivulus* spp. and *Neoheterandria umbratilis* and *N. cana*). In other cases it is unknown whether cognate forms existed in the past in other complexes, *e.g., Cichlasoma sieboldii, C. nicaraguense, C. citrinellum, C. alfari, Alfaro cultratus*). Sympatry between cognates is not always complete (*e.g., Cichlasoma nigrofasciatum* and *C. septemfasciatum* are sympatric in rivers, but only the former has been collected in Lake Nicaragua).

A lineage represented by *Cichlasoma nicaraguense*, which apparently has no extant cognate species in other assemblages, survives only in the San Juan and adjacent Costa Rican drainages. Thus, in this exceptional case, there is no clue to its distribution previous to the formation of the San Juan watershed. The San Juan drainage has become a refuge for several species that have retreated from areas apparently now less suitable. A few endemic species increase the total still more, and will be discussed in the next section.

Descendants of the Atlantic Talamancan Component and their Pacific Talamancan geminate forms reveal that both sides of the Talamancan landmass once had a common freshwater fish fauna. As the Talamancan Cordillera rose and formed part of the Isthmian Link, the Trans-American geminate pairs were pushed apart to occupy the lowlands of opposing slopes. The Pacific slope geminate species were retained in southeastern Costa Rica by the Punta Mala filter-barrier. Only *Cichlasoma sieboldii* has reached the next drainage northward and extended a fair distance into Panamá having reached the Peninsula de Azuero. The Punta Mala headland has been emergent throughout the Tertiary (Dengo, 1962b) and apparently has long been a major impediment to freshwater fish dispersal on the Pacific slope. The Atlantic slope representatives of geminate pairs have remained on the Atlantic slope of Costa Rica and western Panamá and not surprisingly, invaded the Río San Juan watershed or have spread to extreme eastern Panamá (*i.e., Hyphessobrycon panamensis*, Fig. 9).

Poeciliopsis gracilis (Fig. 4), the only species of the genus to reach the Atlantic versant, may have done so through a Río Tamarindo-Lake Managua route when the lake was draining toward the Pacific. The same species also occurs on the Atlantic versant in southern México and Guatemala (Rosen and Bailey, 1963). The gar, *Lepisosteus tropicus* (Fig. 2) which occurs on both slopes of southern México, reaches the Golfo de Fonseca on the Pacific side and also is common in parts of the Río San Juan drainage. *Poecilia* cf *sphenops* occurs on the Pacific slope of northern Central America, but also is found in tributaries of the Great Lakes. The latter two species may have utilized the same route as *P. gracilis* to reach the San Juan.

The two heterandrin genera *Priapichthys* and *Neoheterandria* are closely related and may have arisen on opposite slopes of Central America from a common ancestor. Since the reestablishment of the Isthmian Link, they have spread southward to the Río Atrato and Pacific drainages of northern South America.

The disappearance of the Bolivar seaway sometime during Pliocene allowed members of the New Southern Element to reach Central America for the first time. Both slopes of the isthmian region were inhabited as far north as Punta Mala, Costa Rica on the Pacific side and to the Nicaraguan embayment on the Atlantic slope. Ancestors of *Astyanax fasciatus* and *Synbranchus marmoratus* overcame these filter-barriers sooner than any of the other New Southern members and extended well north. How did the ubiquitous *Astyanax fasciatus* reach the southern United States, leaving behind all other New Southern descendants in Middle America? A combination of generalized ecologic requirements, salt tolerance, large numbers of individuals, a strong migratory proclivity and little ostariophysan competition, I think are the key factors. After the closure of the Nicaraguan marine embayment, *Brycon, Bryconamericus* and *Roeboides* dispersed northward principally along the Atlantic versant; a representative of the latter genus reached the Pacific slope and extended along the narrow Pacific side to southern México. The large ranges of *Brycon guatemalensis* (Fig. 3) and *Roeboides guatemalensis* reflect the geographic stability of the region during Late Pliocene and Pleistocene (*i.e.,* subdivision of these species did not take place). *Carlana* appears to have arrived in lower Central America later, or to have dispersed more slowly, than other New Southern species. Subsequent xeric conditions in Panamá are probably responsible for this differentiation and disjunct species pattern.

Bramocharax shows a disjunct distribution like *Carlana*, but has no known unequivocal South American counterpart of common ancestry (Rosen, 1972). The genus does not display the isthmian species pattern typical of the New Southern Element, but its Guatemalan and Great Lakes disjunct distributions suggest that the lineage has been retreating rather than expanding. It is impossible at this time to confirm whether the genus arose in Central America as suggested by Rosen (1972) or evolved first in South America.

Secondary distributions of San Juan fishes in the Chiapas-Nicaraguan Province have already been discussed. Members of both the Old and New Southern Elements show such Pacific slope distributions and none appear to have deviated greatly from the parent populations, which suggests recent dispersal or perhaps that some degree of interchange still takes place across the continental divide.

Salt tolerance of freshwater fishes is just one of numerous factors that determine their ability to disperse from one watershed to another. A glance at the distribution of the freshwater fishes of South America (Gery, 1969) will suffice to remind one that the distribution of even major groups is far from uniform throughout that continent and that diversity drops off rapidly outside the Amazon Basin.

The two perhaps most ubiquitous freshwater forms in Middle America, *Astyanax fasciatus* and members of the *Mollienesia* species group of *Poecilia,* extend from sea level to altitudes over 1000 meters. This has undoubtedly permitted them to disperse coastwise as well as to utilize headwater stream capture and other means of dispersal. They have probably repeatedly crossed low passes in the continental divide throughout Middle America.

Differential salt tolerance of freshwater fishes often has been proposed to account for the ability of some freshwater

forms to cross the open ocean, and thus reach areas unattainable by other, less salt-tolerant freshwater fishes. Myers (1938), on the basis of present fish distribution, classified families of freshwater fishes into ". . . *primary division* whose members are very strictly confined to fresh water, and a *secondary division* whose members are generally restricted to fresh water but occasionally enter the sea voluntarily for short periods". Myers (1938, 1966) and Darlington (1957) have used this classification to explain the time differential of the arrival into Central America of different families of freshwater fishes from South America. This approach does not explain how the secondary division *Aequidens* and *Geophagus* have only reached Costa Rica and Panamá respectively, whereas *Cichlasoma* has extended to the southern United States. In addition, I do not believe that very many secondary division fishes enter the sea voluntarily. Most Central American freshwater fishes are never found in the lower portion of rivers under tidal influence, but many appear just above this zone. A few such as *Astyanax fasciatus* and *Roeboides guatemalensis* are not uncommon in small tidal streams. Others also occur in brackish lagoons and estuaries (*eg., Poecilia gillii, Gambusia nicaraguensis, Belonesox belizanus* and *Cichlasoma maculicauda*). Other species such as *Brycon guatemalensis, Cichlasoma friedrichsthalii, Lepisosteus tropicus* and *Rhamdia* spp. also may be found in truly brackish biotopes, but although I have seen them very close to the sea, I have never found them in brackish water.

Several authors (Darnell, 1962; Loftin, 1965; Miller, 1966 and Martin, 1972) have pointed out that some primary freshwater fishes have been shown experimentally to be more salt-tolerant than other fishes assigned to the secondary freshwater groups. Myers (1938) himself mentioned that a few ostariophysans enter brackish water briefly and a few families such as Ariidae are found largely in seawater. In spite of these exceptions and based on limited personal experiments, I still feel that Myers's classification reflects real physiological differences within most members of the different families of freshwater fishes. I think that salt tolerance has been an important factor in the *short-range* dispersal of a few species of freshwater fishes, especially those which frequently and voluntarily occur in brackish biotopes. I feel that it does not account for the *long-range* dispersal over the open sea, of entire assemblages of secondary freshwater fishes. I refer in particular to the original species components of the Old Southern Element which probably represent closely those forms existing in northwestern Colombia sometime around the beginning of the Tertiary, and not just salt-tolerant forms which managed to "island hop" across an intercontinental archipelago.

It could be argued that if an ancient transcontinental connection existed, surely some ostariophysans such as *Astyanax* would have reached Central America at that time. Apparently *Hyphessobrycon* and probably *Rhamdia* did form part of the Old Southern Element. *Astyanax* probably evolved later in South America or did not reach northern Colombia in time. It is also interesting that *Astyanax orthodus*[2], a representative of the *Astyanax bimaculatus* species group, reaches only the southern edge of Atlantic Costa Rica. It appears that *A. fasciatus* was among the earliest arrivals of the New Southern Element, but that *A. orthodus* arrived much later or dispersed much more slowly, perhaps due to competition with the previously established *A. fasciatus*. These species represent the two most conspicuous species groups of this dominant South American genus. Yet, they have performed very differently with regard to their invasion of Central America.

Several writers have proposed that the Greater Antilles were united at some time and that this landmass or one of its segments was connected with North, Central or South America at some period from Late Mesozoic to Middle Tertiary. Myers (1938) has cited some of these authors and Rivas (1958) discussed the paleogeographic evidence of a Miocene-Pliocene link between Cuba and Yucatán, and postulated that the Cuban endemic poeciliids of the tribe Girardinini reached Cuba by this route. In addition, Nuclear Central America may have been linked to the Greater Antilles through the "Caribbean Land" which, if it existed, foundered no later than the Miocene (Maldonado-Koerdell, 1964). The Antillean poeciliids and *Cichlasoma* (*Parapetenia* species group) have Central American affinities. Hoedeman (1959) tentatively grouped members of the genus *Rivulus* into species complexes. On the basis of his arrangement, the Antillean species belong to groups with both Central and South American relationships. Thus, Central American freshwater fishes probably populated the Antilles, but *Rivulus* may have done likewise or may have reached Central America from South America via the Antilles as well as through Central America. On the basis of what I have said about salt tolerance in fishes, I feel that a land connection between the Antilles and Central America was essential to account for its freshwater fish fauna.

Dr. Leon Croizat's principal publications on biogeographic subjects have not been available to me, but he has kindly offered the following observations on the final draft of this paper. He considers (*in litt.*) the Old Southern Element a remnant of a much larger ichthyofauna which once inhabited a land which united the Greater Antilles and Central America. He disagrees that the New Southern Element is of Late Tertiary age, but believes that it is a northward extension of an ancient ichthyofauna that inhabited former landmasses in the eastern Pacific Ocean that united México, Central America and South America.

I agree with an early Central American-Antillean connection, but feel that the New Southern Element arrived long after former Pacific landmasses subsided. The Late Cretaceous volcanic corridor between lower Central America and South America (Fig. 5) could represent part of this ancient Pacific landmass, but I believe that it provided passage north for the Old Southern Element.

In summary, the Old Southern Element, composed of poeciliids, a few lineages of *Cichlasoma, Rivulus, Gymnotus,* the characid *Hyphessobrycon* and probably *Rhamdia,* migrated northward into the freshwater vacuum of Central America. After a long period of isolation, a second quite different element composed of several characoid families, a synbranchid, armored catfishes, trichomycterids, gymnotids, *Aequidens* and *Geophagus,* has begun to supplement the original ichthyofauna. Of this New Southern Element, only a handful of characids and a synbranchid eel have reached the San Juan Province. Subsequent to subdivision of these elements, secondary dispersal has occurred to the north, south and across the Continental Divide. A northern element, *Lepisosteus*, and some poeciliid lineages appear to be extending southward, only two reaching South America. There is evidence that poeciliids, *Cichlasoma*, and one or more lineages of *Rivulus* reached the Antilles by way of a land connection with Central America. Other *Rivulus* may have reached the Antilles directly from South America.

[2]A new record for Costa Rica.

Derivation of the Rio San Juan Ichthyofauna

The Great Lakes fish fauna is the result of the fusion of two faunas. A rather homogeneous Atlantic slope element was long subdivided by a marine portal, and later by an embayment. Part of this same geologic depression, now filled with fresh water, provides an especially suitable habitat where many species from each of the formerly isolated components now overlap. Thus, on the basis of conclusions reached in the study, the majority of the San Juan basin fauna developed outside of the present watershed by means of allopatric speciation. It is now necessary to consider the forms endemic to the Great Lakes. Two of these nominal species are of marine affinities and have not been mentioned previously. The *sabalete* (*Dorosoma chavesi*) is now restricted to the Great Lakes, but it and its geographically nearest congener, *D. petenense,* which reaches its southern limit in British Honduras, were obviously descended from common stock. We have no way of knowing if *Dorosoma* was subdivided by one of the past marine embayments before it disappeared from Honduras and northern Nicaragua, but the end result has been the same: the southernmost species has evolved into a distinct form isolated from its congeners.

The lake endemic *Melaniris sardina* and riverine *M. chagresi* are reported to be geographically isolated, although crucial regions like the Río San Juan proper have scarcely been sampled. The latter species has been reported from tributaries to the Río San Juan southward to eastern Panamá. Each population is clearly subject to quite different environmental pressures and the morphologic differences reported for them are to be expected. Future study will reveal if this is a type of headwater isolation involving a single species, or if they represent two reproductively isolated populations.

The lacustrine *Astyanax nasutus* is syntopic with *A. fasciatus* only at certain littoral habitats in Lake Nicaragua. The incipient speciation taking place now between the lake and stream populations of *A. fasciatus* suggests how *A. nasutus* may have evolved from an *A. fasciatus*-like ancestor. The *chulín* (*Rhamdia* sp.) has adapted to the deepest waters of Lake Nicaragua and possibly evolved there. Further study is required to determine the systematic status of the other endemic catfishes. The lacustrine *mojarras, Cichlasoma labiatum* and *C. citrinellum,* are apparently ecologically separated in Lake Nicaragua. *C. citrinellum* is found in tributaries of the Río San Juan but is also quite common in the Lakes. *C. labiatum* is almost entirely confined to the lake environment. This may be a case of intralacustrine speciation in the true sense.

Lake Nicaragua surely does not have a saturated fish fauna, and in an undisturbed state would eventually produce a more diverse assemblage. The vast Nicaragua-Honduras lowland plain probably never had a diverse ichthyofauna. Part of that fauna has found refuge in the more diverse environment of the Río San Juan basin, but other forms have apparently become extinct.

Chronological Implications of San Juan Fish Evolution

There is no evidence of "explosive evolution" in the Great Lakes of Nicaragua. Nevertheless, the lakes have played a role in the speciation of a few San Juan fishes and have served as a refuge for other apparently displaced species. With two exceptions, evolution has not transcended the species level in the region and most of the lake forms also occur in appropriate habitats in adjoining tributaries. This rather unspecialized fauna certainly is not of great age.

Unfortunately there is no simple correlation between time and intensity of speciation. Briggs (1966) cited evidence of the exceedingly variable evolutionary rate in different situations.

Data about two other tropical lakes is pertinent to the present problem. Lake Gatún, Panamá, was created in 1914 by damming the Río Chagres which drained the Atlantic side of the present Canal Zone. About 34 freshwater fishes are known from the drainage. Hildebrand (1938, 1939) recorded 24 species from the lake, only 4 of which were of marine affinity. Characids accounted for nearly half of the total. A large proportion of the Chagres fauna then, was able to adapt rapidly to the virgin lacustrine environment.

The following data were taken from Fryer and Iles (1972). Lake Albert, one of the rift-valley lakes of central Africa, is roughly the same shape and depth (58 meters maximum) as Lake Nicaragua, but is somewhat smaller (6,800 km^2). It drains into the Nile and is estimated to have acquired its present characteristics during Middle Pleistocene (500,000 years ago). Its fishes total 45 to 48 species of which 7 or 8 are endemic forms. Cichlids, a dominant element in many of the rift lakes, number only 9 or 10 species in Lake Albert. The similarity between the gross physical aspects and numbers of total and endemic species in Lake Albert and Lake Nicaragua is striking, although the ichthyofauna of each lake was probably arrived at in quite different ways.

It is unknown if the most common very large predator, the *pez sierra (Pristis perotteti)*, has had an effect on speciation in Lake Nicaragua. Authors differ as to whether predation increases or decreases speciation of prey species (Fryer and Iles, 1972), and the matter is still far from settled.

On the basis of the above very indirect evidence, I suspect that the Great Lake of Nicaragua formed between one-half and one million years ago. As soon as a freshwater lake was formed, fishes inhabiting the surrounding tributaries populated it. Subsequently, fishes previously isolated from each other to the north and south mixed for the first time in the habitat.

The freshwater fishes of Atlantic slope origin found on the Pacific versant of Nicaragua are phenotypically similar to the Great Lakes populations. If their presence on the Pacific side is not a result of human introduction, it is obvious that they came from a single large lake draining toward the Pacific until recently. This large lake would have been about 15 meters higher than now and already had a diverse Atlantic slope fauna. It is necessary then to assume that at some time the original Atlantic discharge of the lake was blocked by tectonic movements near the outlet, causing the lake level to rise and a new Pacific outlet to form. Later the Río San Juan connection was reformed and the level gradually dropped and two lakes were formed. The fact that one or two fishes in an isolated crater lake on a peninsula in Lake Managua (Lago de Xiloá) have diverged considerably from the Lake Managua population (Villa, 1968) does not necessarily detract from the hypothesis that a single lake was draining into the Pacific until recently. Fryer and Iles (1972) cite studies by P. H. Greenwood and E. Trewavas which strongly suggest that speciation of the cichlid genus *Haplochromis* has occurred in about 4000 years in Lake Nabugabo, a small lake cut off from Lake Victoria, Africa.

Unlike those fishes of Atlantic slope origin on the Pacific side of Nicaragua, the descendants of the Talamancan Complex have been isolated by the Cordillera for a considerably longer period. These Trans-American species pairs exhibit about the same degree of differentiation as their marine counterparts.

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SUMMARY

On the basis of recent collections in lower Middle America, the San Juan Fish Province is delimited for the first time. The northern boundary includes the Río Prinzapolka drainage in Nicaragua, and the southern limit occurs in western Panamá between Peninsula Valiente and Río Coclé del Norte. Punta Mala on the Pacific versant of Costa Rica is indicated as an exceptionally effective filter-barrier that demarcates the Chiapas-Nicaraguan and Isthmian Provinces. The San Juan assemblage consists of 8 families, 25 genera, and 54 species of freshwater fishes and is thus less diverse in all of these taxa than the Usumacinta and Isthmian assemblages. Only the Chiapas-Nicaraguan assemblage has fewer genera and species.

Substrate specificity limits the distribution of cichlids in Lake Nicaragua and two species of catfish (*Rhamdia*) have different depth preferences. The characid *Astyanax fasciatus* is most common in sheltered inshore waters, but *Astyanax nasutus* frequents gravel beaches and is the dominant limnetic species. One or two species of polymorphic cichlids, which exhibit rubrism and variable lip development, abound in the lake, but striking specializations have not yet been developed by other species.

The geographic distribution of monophyletic lineages of San Juan freshwater fishes reveals two basic patterns which correspond to one ancient and one much more recent, faunal element which reached Central America from the south. The present analysis considers that virtually all freshwater fishes, regardless of their salt tolerance, required a landbridge to reach Central America. Sketchy geologic evidence of an early intercontinental land bridge suggests that an Old Southern Element probably reached the region during the Late Cretaceous or Paleocene. On the basis of present fish distribution, there is no reason to suspect that Central America was not isolated from South America by a marine portal or marine portals from Eocene to Pliocene times as has been frequently proposed by both geologists and biologists. Geologic evidence suggests that a New Southern Element must have reached Central America no earlier than the Pliocene.

Most lineages composing the Old Southern Element have extended throughout Middle America or farther north, primarily on the Atlantic versant. Two Upper Tertiary marine embayments, the Amatique and Nicaraguan basins, have subdivided this element into three segments: the Western Nuclear Central American, Eastern Nuclear Central American and Talamancan Complexes. The result of the isolation and subsequent differentiation of each complex has allowed numerous unrelated lineages to develop different cognate species in each complex. In Middle to Late Tertiary another marine embayment, the Mosquitia basin, has influenced fish distribution within the Eastern Nuclear Central American Complex. Since disappearance of these barriers, the descendent species have dispersed somewhat, sometimes resulting in the replacement of one member of a cognate or the sympatry of both members. Sympatry of cognate pairs accounts in part for the relatively high species diversity of the Río San Juan watershed. This basin has also served as a refuge for other species which presumbably disappeared from their former ranges to the north or south. Six species endemic to the Great Lakes boosts the total number of freshwater fishes in the Río San Juan drainage basin to 46 species.

The above account presupposes the existence of emergent landmasses southeast of the Nicaraguan Depression at least throughout the latter half of the Tertiary, a reality which has only recently been supported by geological evidence. One of these landmasses, the Talamancan Island, upon incorporating into the emerging Isthmian Link in the Late Pliocene, has given rise to several cognate species pairs which now inhabit opposing sides of the continental divide. These Trans-American geminate species show approximately the same degree of differentiation as the many Trans-American marine geminate forms.

The New Southern Element is represented in the San Juan Province by only a few lineages. These groups are characterized by considerable species differentiation in the isthmian region and by seldom more than one species north of Costa Rica. The Pliocene-Pleistocene events which produced this isthmian pattern of speciation and the numerous other groups which have as yet only reached Panamá, are not considered.

A Northern Element is represented by one species, *Lepisosteus tropicus*, in the San Juan Province. Headwater stream capture has been important in permitting members of the San Juan assemblage an access to the Pacific versant and perhaps allowing three Pacific-slope species to reach the Atlantic versant. Evidence suggests that Lake Nicaragua and Lake Managua were once a single lake which drained toward the Pacific Ocean. On the basis of indirect evidence and the low degree of endemism in the Great Lakes, the lakes and their fauna are estimated to be between one-half and one million years old.

Resumen

El análisis de la distribución actual de los peces dulceacuícolas centroamericanos permite fijar los límites de Mesoamérica. La Provincia Ictica de San Juan está delimitada al norte por la cuenca del Río Prinzapolka y su límite Sur se localiza en Panamá occidental entre Península Valiente y el Río Coclé del Norte.

Ocho familias, 25 géneros y 54 especies de peces dulceacuícolas, y por lo menos 84 especies de afinidad marina, habitan la Provincia Ictica de San Juan.

Algunos peces tales como cíclidos y unos carácidos (*Astyanax fasciatus* y *A. nasutus*) están limitados a ciertas regiones del Lago de Nicaragua debido a la diferencia en substrato u otros factores. Dos especies de *Rhamdia* apparentemente ocupan hábitats a profundidades diferentes.

La distribución geográfica de líneas monofiléticas (tribus, géneros o complejos de especies) de peces dulceacuícolas del San Juan, presenta dos patrones básicos que corresponden a un elemento faunístico antiguo y otro mucho más reciente, los cuales llegaron a América Central desde el Sur.

Se considera en este análisis que casi todos los peces de agua dulce, prescindiendo de su tolerancia de salinidad, requirieron de un puente terrestre para llegar a América Central.

Evidencia geológica incompleta de un puente terrestre intercontinental antiguo sugiere que probablemente llegó un Elemento Meridional Antiguo a la región durante el Cretácico Superior o en el Paleoceno. La mayor parte de los linajes que comprende este elemento se ha extendido a través de Mesoamérica o más al norte, principalmente en la vertiente atlántica. Dos entradas de mar durante el Terciario Superior, las cuencas Amatique y Nicaragüense, dividieron este elemento en tres segmentos: los Complejos de Mesoamérica Nuclear Occidental, Mesoamérica Nuclear Oriental y Talamanca. El resultado del aislamiento y la diferenciación posterior de cada complejo ha permitido a varios linajes no relacionados producir diferentes especies gemelas en cada complejo. En el Terciario Medio y Superior, otra entrada de mar, la cuenca Mosquitia, afectó la distribución de peces en el Complejo Mesoamericano Nuclear Oriental. Al desaparecer estas barreras, las especies que evolucionaron en cada complejo se dispersaron y permitió a veces la sustitución de una de las especies gemelas por la otra o la simpatría de dos especies gemelas. Este último fenómeno explica en parte la diversidad relativamente alta en la cuenca hidrográfica del Río San Juan. Esta cuenca también ha servido de refugio para otras especies que ahora no se encuentran en ninguna otra parte.

La distribución actual de peces apoya la teoría de que Centroamérica y Sudamérica se encontraban separadas por el mar desde el Eoceno hasta el Plioceno.

Según evidencia geológica el Elemento Meridional Nuevo debe haber llegado a Centroamérica no antes del Plioceno. Sólo pocas líneas de este elemento se encuentran en la Provincia Ictica de San Juan. Estos linajes demuestran bastante diferenciación en la región ístmica, pero pocas especies al norte de Costa Rica.

El Elemento Septentrional tiene un representante, *Lepisosteus tropicus*, en la Provincia Ictica de San Juan.

Una masa de tierra emergente al sureste de la Depresión de Nicaragua, es una realidad apoyada por evidencias geológicas recientes, por lo menos durante la mitad superior del Terciario. Al formarse parte del Istmo Centroamericano durante el Plioceno Superior, una de estas masas terrestres, produjo varias especies de peces gemelas que ahora habitan en los lados opuestos de la división continental. Estos pares transamericanos demuestran aproximadamente el mismo grado de diferenciación que presentan los pares gemelos transamericanos de agua marina.

La distribución actual de los peces dulceacuícolas indica que los lagos de Nicaragua y Managua eran un solo lago que antes tenía una salida hacia el Océano Pacífico.

Con base en evidencias indirectas y en el bajo grado de endemismo en los grandes lagos nicaragüenses, se estima que su edad debe variar entre medio millón y un millón de años.

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